

# Relationships and Classification of the Pseudopomyzidae (Diptera: Neriioidea)

DAVID K. MCALPINE

Australian Museum, 6 College St, Sydney 2000

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Some groundplan character states of the Neriioidea are examined with special reference to the morphology of the Pseudopomyzidae. The Heleomyzidae are interpreted as a closely related outgroup to the Neriioidea. The Neriidae are possibly the sister group to the Pseudopomyzidae. Groundplan characters of the Pseudopomyzidae are reviewed. Although of small morphological diversity, there are few apparent autapomorphies for the family. The seven recognized pseudopomyzid genera are placed in three informal groups, though the monophyly of these is imperfectly demonstrated.

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## INTRODUCTION

The aim of this paper is not to present a taxonomic revision of the Pseudopomyzidae, but to look at their principal morphological features, in order to establish family limits and relationships and to contribute to an understanding of the nerioid groundplan. Because the pseudopomyzids appear to be particularly primitive representatives of the Neriioidea, this study has the potential to throw some light on the origin and phylogeny of the superfamily.

This group has been given family status by D. McAlpine (1966, 1994), Hennig (1969 and elsewhere), and Krivosheina (1979). I initially pointed out significant resemblances to the Cypselosomatidae and therefore referred the Pseudopomyzidae to the superfamily Micropezoidea (now termed Neriioidea on grounds of priority). Griffiths (1972) merged the Pseudopomyzidae with the Cypselosomatidae and was followed by others, notably J. McAlpine (1989). As there are some impressive and consistent differences between Cypselosomatidae s.str. and Pseudopomyzidae, and because I question the validity of their supposed synapomorphies, I retain family status for Pseudopomyzidae.

The living Pseudopomyzidae are distributed in the Palaearctic Region (*Pseudopomyza* Strobl and *Polypathomyia* Krivosheina), Oriental Region (*Tenuia* Malloch — Philippines), Australasian Region (*Pseudopomyza*), and the Neotropical Region (*Latheticomyia* Wheeler, *Heloclusia* Malloch, *Pseudopomyzella* Hennig, *Pseudopomyza*, the first extending into the United States). A satisfactory key to living genera has been given by Krivosheina (1979).

The biology of the Pseudopomyzidae is very little known. Krivosheina (1979, 1984) recorded the larvae of *Polypathomyia stackelbergi* Krivosheina living under the bark of rotting logs of several tree species. Frey (1952) stated that the adults of *Pseudopomyza atrimana* (Meigen) gather in the afternoon over rotting logs in Finland, a habit which suggests a similar larval habitat to that of *P. stackelbergi*.

## VALUE OF CLADISTIC INVESTIGATION

The basic philosophy of Hennig's phylogenetic systematics is now so widely recognized as based on simple logic that it influences most current systematic research. But the cladistic methodology which grew out of Hennigian thinking is often treated as an arbitrary formula to be applied to every problem in taxonomy, without consideration of the relevance of the data. Some of my taxonomist colleagues reject cladistic method as incapable of revealing facts of any significance or as too difficult to apply in their own research fields.

To me, the value of cladistic research must depend on the answers to certain fundamental questions. Question 1: Will evolutionary processes leave us with one or more identifiable apomorphies to indicate each internode of the evolutionary tree? The answer depends on the answer to two further questions. Question 2: Will one or more distinctive apomorphies be produced for most internodes? Question 3: If such apomorphies are produced, will they be retained in a recognizable form in sufficient descendent taxa to be recorded by taxonomists? A negative answer to question 2 may result from evolutionary conservatism, or brevity of internodal time, or a combination of these two factors. A negative answer to question 3 may result from masking of particular apomorphies by subsequent evolutionary modification. The general answer to questions 2 and 3 therefore is: 'Sometimes', or 'In a proportion of cases'. The answer to question 1 therefore must be: 'In a proportion of a certain proportion of internodes', with no certain method of generalising as to the value of the final proportion of internodes. All post-Hennigian cladistic methodology depends on the answer to question 1 being rather strongly positive (though not necessarily absolutely so). As the general answer is not very positive, we can only expect the resolution of nodes in a cladogram to be sometimes right, sometimes wrong. The assertion, that use of a large number of characters in cladistic programs tends to neutralise homoplastic errors, is unconvincing. If the evidence for monophyly at a node is not preserved in the study specimens no amount of loading morphological noise into a computer program will resolve the problem.

I therefore believe that the indiscriminate use of morphological data without very careful and informed evaluation is unlikely to produce a cladogram of any complexity which accurately indicates the phylogenetic tree, and it may not necessarily indicate an approximation to the true tree.

I incline to accept some strongly characterised taxa, even though not supported by identifiable autapomorphies, for the reason that lack of obvious autapomorphies is not proof of polyphyletic (or paraphyletic) status. Their likelihood of being monophyletic may be greater than that of some taxa based only on weakly hypothetical autapomorphies. The family Pseudopomyzidae, the monophyly of which is only weakly evidenced by apparent autapomorphies, is therefore retained.

A problem in cladistic method is multiple character convergence between taxa, which can be difficult to distinguish from multiple synapomorphy. This has led to such unjustified taxa as 'Micropezoidea s.str.' and the 'indubitably monophyletic' Megamerinidae of Hennig (1958, 1965), both re-evaluated in my current research.

Selection-directed multiple convergence is, however, only one of the possible causes of error through reliance on statistical parsimony. Some kinds of characters are inherently unstable (e.g. characters commonly involved in niche divergence following speciation, and characters involved in sexual selection), so that lack of change in these, through a series of speciation events, is relatively improbable.

I believe that Hennigian logic can produce some viable theories about phylogenetic relationships when the data are carefully considered with due regard to major stable outgroups (rather than minor unstable ones), to overall stability of character states, and to likelihood of simple reversals with reversal of selection pressure. My experience suggests that some groups are far more amenable to cladistic treatment than others.

On firmer ground than generation of cladograms, can be some attempts to determine monophyletic taxa and their sister groups. In his many papers dealing with phylogeny of Diptera, Hennig often limited himself to the latter kinds of conclusion and only rarely produced detailed cladograms.

## RELATIONSHIPS

The Pseudopomyzidae have been consistently placed in the Neriioidea (Micropezioidea) in modern phylogenetically based classifications. Other generally included families are Cypselosomatidae, Neriidae, Micropezidae s.l., and I now confirm the inclusion of the Megamerinidae, but the evidence for this will be published elsewhere.

The family Pseudopomyzidae possesses the following features which are distinctive groundplan conditions for the superfamily and are, to a certain extent, also diagnostic features for it. They are apomorphic in relation to the groundplan of Schizophora and are probably autapomorphies for Neriioidea.

- 1). Face desclerotized on lower part medially. Despite the statement of Hennig (1971b: 5) to the contrary, a desclerotized zone of variable extent and often of triangular shape on the lower part of the face is the general condition of the Neriioidea, occurring as the predominant condition in all five families, though there is some apparently secondary sclerotization in *Cypselosoma* s.str. and the majority of the micropezid subfamily Taenapterinae. Even in these latter categories there is often clear differentiation between a lightly sclerotized median zone and heavily sclerotized lateral parts of the face.
- 2). Male postabdomen with elongate, ventrally channelled epandrium having a pair of terminal surstyli and cerci; also elongate basiphallus supported by usually two pairs of longitudinal sclerotized rods, with a pair of preapical processes and a terminal, anteriorly directed elongate distiphallus, with flexible apex (see Hennig 1969).
- 3). Female postabdomen: segment 7 longer than preceding segments, with fused tergite and sternite, forming an ovipositor sheath or oviscape; segment 8 with tergite and sternite desclerotized. This set of characters (3) is not present in Megamerinidae.

A further possible groundplan apomorphy for Neriioidea is: accessory glands of female reproductive system absent. This is suggested by my dissections of *Pseudopomyza collessi* McAlpine, *Clisa australis* (McAlpine) (Cypselosomatidae), *Telostylinus angusticollis* (Enderlein) (Neriidae), and of *Metopochetus* sp. (Micropezidae, Eurybatinae) by M.A. Schneider in my laboratory.

## Outgroups of the Neriioidea

In order better to understand character polarities and their significance for classification in the families of Neriioidea, knowledge of the sister group or, at least, one or more closely related outgroups of the Neriioidea would be helpful.

J. McAlpine (1989) has indicated in a cladogram (his fig. 116.2) a sister group relationship between the Neriioidea and Diopsoidea, but gave no supporting discussion in the text. The synapomorphies supporting this alliance given on the cladogram are: body form slender; Sc and R<sub>1</sub> approximated; pterostigma lost; A<sub>2</sub> reduced. These are character states so widely present and of such frequent arisal among acalyptrate schizophorans as to carry almost no conviction for supporting monophyly in this case. I have seen certain representatives of the Heleomyzidae, Clusiidae, Chloropidae, Teratomyzidae, Asteiidae, and other families that combine these character states.



Furthermore, some nerioids, such as *Cypselosoma* and certain pseudopomyzids, are not particularly slender in habitus (probably primarily robust), and some forms placed in Diopsoidea (e.g. the Tanypezidae and *Gobrya*) and in the Nerioidea (megamerinids and numerous micropezids) have as great distal divergence between Sc and vein 1 ( $R_1$ ) as do many of the Sciomyzoidea. In the apparent groundplan of the Micropezidae vein 7( $A_2$ ) is not greatly reduced. For these reasons I consider that no acceptable evidence has been produced to demonstrate the probability of a close relationship between the Nerioidea and Diopsoidea.

J. McAlpine (1989) considers that the Nerioidea have retained more plesiomorphic conditions in their groundplan than any other acalyptrate superfamily. However, I regard some of these character states as not demonstrably plesiomorphic or probably not present in the groundplan of the Nerioidea. The large 'relatively unmodified' male sternite 6 present in many Nerioidea may not be the groundplan condition of the Schizophora. My studies of both Heleomyzidae (McAlpine 1985) and Neurochaetidae (McAlpine 1988) seem to indicate that what is effectively a large median ventral sternite 6 in a few representatives of these families is an apomorphic effect and that sternite 6 is primarily very asymmetrical in both families. It may well be asymmetrical both in position and shape in the groundplan of Schizophora, judging both from comparative morphology within the Schizophora and comparison with the outgroup Syrphoidea. Furthermore the conditions of undeveloped vibrissa, apical to subapical arista, unbroken costa, and long, acute cell cup I do not consider to be in the groundplan of the Nerioidea, for reasons given below.

The families Pseudopomyzidae and Cypselosomatidae include those nerioids with habitus most like that of numerous conventional schizophorans which are probably of more or less plesiomorphic habitus for the Schizophora. They also possess such normal attributes of other acalyptrate superfamilies (outgroups in the broad sense) as a series of postocular setulae, a strongly differentiated vibrissa, a presutural bristle, two notopleural bristles (anterior and posterior), and an apical ventral spur on the mid tibia. I consider these attributes most likely to represent groundplan states for the Nerioidea, in addition to the more generally accepted ones given above. Because the costal break near the end of the subcosta is characteristic of these families (often occurring as a trace also in the Neriidae) and contributes to overall resemblance to possibly related outgroups (see below), I regard its presence as a groundplan character state for the Nerioidea, and the closing of the break as an apomorphy, where it occurs in this superfamily.

Before the significant attributes of pseudopomyzids and cypselosomatids were understood, their component genera were placed by competent dipterists in or near several other schizophoran families. I consider that it may be profitable to explore similarities of these nerioid taxa to the Clusiidae (where Hennig, 1948, provisionally placed the cypselosomatid taxa) and to the Heleomyzidae (in or near which pseudopomyzid taxa have been placed by Malloch 1933, Hennig 1958, and Harrison 1959).

Cypselosomatids show some clusiid-like features, including the following: postvertical bristles usually divergent; vibrissa distinct; face more or less desclerotized; fronto-orbital bristles in a well developed series, reaching well forward on postfrons; costa broken only near end of subcosta; vein 7 ( $A_2$ ) not extending beyond alula. In addition the aedeagus of *Clusia lateralis* (Walker) as shown by Soós (1987, fig. 70.9) is remarkably similar to that of *Clisa* (D. McAlpine 1966, fig. 1d, as *Cypselosoma*), and to that of some other nerioid flies. Other clusiid genera have diverse and often very different aedeagi, but in *Tetrameringia* (see D. McAlpine 1960, fig. 26) the aedeagus approaches that of *Clusia* to some extent. Possibly, then, the resemblance between the aedeagi of *Clusia* and cypselosomatids is coincidental convergence. I also think that the other above points of resemblance may not be adequate to support a theory of close relationships between the Nerioidea and the Clusiidae.

The general characters of the Pseudopomyzidae which resemble those of the Heleomyzidae (or many heleomyzids) include the following: postvertical bristles conver-

gent; fronto-orbital bristles in a simple series, reclinate; vibrissa distinct; arista inserted dorsally; costa broken near end of subcosta, with one or two differentiated bristles before break; costa with spaced anterior to anteroventral spines or spinules on section bordering marginal cell ( $r_1$ ) (e.g. *Heloclusia*, *Latheticomyia*, *Polypathomyia*); anal cell (cup) relatively short, not acute; fore femur with seriate dorsal and posteroventral bristles; mid tibia with large apical ventral spur; fore basitarsus with male-restricted terminal ventral process (in *Polypathomyia stackelbergi* Krivosheina, *Latheticomyia tricolor* Wheeler, and *Heloclusia imperfecta* Malloch); mid basitarsus longer than fore basitarsus.

The modification of the male fore basitarsus has been previously mentioned (D. McAlpine 1991) as occurring in certain taxa of Heleomyzidae, Sphaeroceridae (both Heleomyzoidea), Dryomyzidae, Helcomyzidae, and Coelopidae (Sciomyzoidea), but its presence in the Neriioidea has been overlooked, except by Wheeler (1956). I have not seen the modification in nerioid genera other than *Heloclusia*, *Latheticomyia*, and *Polypathomyia* (Pseudopomyzidae), and perhaps *Cliobata raptimanus* (Bezzi) (Micropezidae, Taeniapterinae). The modification in the male of *C. raptimanus* (see Aczél 1951: fig. 15) looks so different that it may not be homologous. Otherwise, it is probable that this male basitarsal modification is a single origin structure present only in the superfamilies Sciomyzoidea, Heleomyzoidea (or Sphaeroceroidea), and Neriioidea. However, evolutionary loss of the modification must have occurred in many lineages, and its presence in some taxa may be due to reactivation of old genetic material. It therefore has limited usefulness as an indicator of relationships. The wideness of occurrence of the modification seems to indicate that the trait was acquired in an ancient common ancestor of the three superfamilies, and this ancestor may also have been ancestral to certain other at present unidentified taxa of Schizophora.

Because of the above points of resemblance between the Pseudopomyzidae, as a somewhat primitive nerioid group, and the Heleomyzidae, I regard the Heleomyzoidea as probably a closely related outgroup of the Neriioidea, perhaps its sister group. For this reason comparison of nerioid taxa with the Heleomyzidae appears to have some validity for determining character polarities in the Neriioidea, and my interpretations therefore often differ from those of Hennig (1958), Aczél (1959), J. McAlpine (1989).

### Relationships to other nerioid groups

A relationship between Pseudopomyzidae and Cypselosomatidae has often been postulated and some have suggested that the two families should be merged (see above). The latest argument for combining these groups (as two subfamilies of Cypselosomatidae) gives the following autapomorphies for Cypselosomatidae s.l. (J. McAlpine 1989): (1) vibrissa developed; (2) arista arising dorsobasally; (3) costa with subcostal break; (4) costagial bristle very strong; (5) male with strong paired bristles on sternite 8 and epandrium; (6) female with two spermathecae. In accordance with my theory of the Heleomyzoidea as an outgroup for the Neriioidea, characters 1–4 are likely to be groundplan plesiomorphies for the Neriioidea and not autapomorphies of any of its component groups. Condition 4 occurs in many taxa of Micropezidae and Neriidae and is probably a groundplan plesiomorphy in each family. The paired bristles on male sternite 8 and the epandrium (character 5) possibly represent a homologous groundplan condition for both Pseudopomyzidae and Cypselosomatidae s.str., but this does not necessarily place the condition as a synapomorphy (autapomorphy for Cypselosomatidae s.l. in J. McAlpine's terminology). There is really no evidence that this condition does not date from an earlier stage in nerioid evolution, perhaps even in the groundplan of the Neriioidea. It would, then, have been secondarily lost in other nerioid lineages, a not improbable event in view of the inherent instability in male postabdominal characters and the fact of the absence of these bristles in some pseudopomyzids.

The number of spermathecae (character 6) is often unstable within the more mor-



phologically diverse schizophoran families (e.g. Heleomyzidae, Carnidae, Coelopidae, Tephritidae). Hennig's (1969) descriptions of pseudopomyzid spermathecae suggest instability in the family (two of similar size present in *Pseudopomyza* (*Rhinopomyzella*) *nigri-mana* (Hennig), two, of which one appears to be vestigial, in *P. (R.) albinana* (Hennig), 'Spermatheken habe ich nicht gefunden' in *Latheticomyia longiterebra* (Hennig). *Pseudopomyza collessi* and the cypselosomatid *Clisa australis* each have two similar spermathecae with lightly sclerotized vesicles (D. McAlpine 1993, 1994). In the Micropezidae three spermathecae are reported for *Compsobata univitta* (Walker) (Sturtevant 1925), *Calobata petronella* (Linné) (Hennig 1958, as *Trepidaria* sp.), *Calycopteryx mosleyi* Eaton, and for *Metopochetus* sp. (author's observations). According to Freidberg (1984), *Micropeza* (three species examined) has three normal spermathecae and a fourth of unusual structure. Dufour (1851) has reported two spermathecae for '*Calobata cothurnata*' (perhaps *Compsobata cibaria* (Linné)), a count that has been queried, but not refuted, by Sturtevant. In the Neriidae, *Telostylus angusticollis* (Enderlein) perhaps has only two spermathecae (author's dissection of an immature female), but Steyskal (1987) gives in the family description of Neriidae 'two pairs of colorless spermathecae present.' Perhaps this statement is based on *Odontoloxozus longicornis* (Coquillett), the best known nearctic species. In view of the frequency of arisal of a spermathecal count of two in the Schizophora, the very few recorded spermathecal counts in the Neriodea, and the apparent variability in the three nerioid families for which more than one species has been investigated, it is not reasonable to regard the spermathecal count of two as necessarily a synapomorphy for Pseudopomyzidae + Cypselosomatidae.

Griffiths (1972) gives a further three 'apomorphous conditions' for Cypselosomatidae s.l. (including Pseudopomyzidae), all characters of reduction in wing venation, two of which are excluded by J. McAlpine (1989) on account of further evidence of the probable groundplan condition of the 'Pseudopomyzinae' (the family Pseudopomyzidae as here delimited). The third character state, 'Subcosta reduced, failing to reach wing margin as distinct vein,' applies to most species of both Pseudopomyzidae and Cypselosomatidae s.str., but not so clearly to *Polypathomyia stackelbergi*, in which the termination of the subcosta differs only slightly from that of some Neriidae. There is thus considerable variation in the extent of subcostal reduction in the Pseudopomyzidae, and reduction of the subcosta is one of the most frequently derived apomorphies known in the Schizophora. One should not therefore found a theory of monophyly of Pseudopomyzidae + Cypselosomatidae on this character alone.

From the above it is clear that evidence for synapomorphy between the Pseudopomyzidae and Cypselosomatidae is at best quite weak, and, as has been shown by Andersson (1976) and Krivosheina (1979), the two groups are strongly differentiated. The resemblance between these families is largely or entirely due to a combination of symplesiomorphy and convergence.

## Some groundplan character states of the Pseudopomyzidae

### I. Characters retained from groundplan of Neriodea.

- (a) Postvertical bristles convergent.
- (b) Fronto-orbital bristles in a simple reclinate series.
- (c) Vibrissa well differentiated.
- (d) Seriate postocular setulae present.
- (e) Face desclerotized on lower median part.
- (f) Arista (antennal segment 6) with extensive non-seriate short hairs.
- (g) Dorsocentral bristles in a complete series.
- (h) Propleural (proepisternal) bristle distinct.

- (i) Upper anterior and posterior sternopleural bristles present.
- (j) Anterior intra-alar bristle (close behind transverse suture) absent.
- (k) Membranous cleft of mesopleuron meeting anterior section of sternopleural (anapleural) suture at a right angle or acute angle.
- (l) Fore femur with elongate dorsal and posteroventral bristles.
- (m) Mid tibia with large apical ventral spur.
- (n) Tarsi cylindrical, not depressed distally.
- (o) Fore basitarsus with male-restricted terminal ventral process.
- (p) Mid basitarsus more elongate than fore basitarsus.
- (q) Costa with subcostal break and pair of bristles at basal side of break.
- (r) Anterodorsal and anteroventral costagial bristles large, latter not basad of former.
- (s) Costa with spaced anterior to anteroventral spines among the hairs.
- (t) Posterodistal angle of discal cell not obtuse, with vein 4 ( $CuA_1$  or  $M_4$ ) extending well beyond angle.
- (u) Basal crossvein (bm-cu or base of  $M_{3+4}$ ) separating second basal (bm) and discal cells.
- (v) Anal crossvein (transverse section of  $CuA_2$ ) recurved.
- (w) Alula forming a prominent lobe.

This set of characters includes those used above as evidence for a relationship between Neriioidea and Heleomyzoidea together with other groundplan characters which are plesiomorphic relative to those of certain other nerioid taxa.

## II. Characters apomorphic in relation to groundplan of Neriioidea.

- (a) Antenna porrect.
- (b) Arista inserted mid-dorsally to subapically on antennal segment 3.
- (c) Subcosta reaching costa very close to vein 1 ( $R_1$ ), the intervening membrane distally indistinct.
- (d) Distal section of vein 7 ( $A_2$ ), beyond alular incision, absent without trace.

The shortness of this list is in accordance with the theory that the Pseudopomyzidae are morphologically closer than other families to the groundplan of the Neriioidea. Although there are numerous differences between the Pseudopomyzidae and Neriidae, these mostly concern the well developed autapomorphies of the Neriidae as compared with the Pseudopomyzidae. Characters II(a) and II(b) above possibly represent intermediate states in their respective character sequences between the nerioid groundplan condition (probably close to that of *Cypselosoma* species) and the more advanced condition seen in the Neriidae. The most plausible autapomorphy for the Pseudopomyzidae is still the reduction of the subcosta. In the Neriidae the subcosta is complete, well sclerotized throughout, and terminates separately in the costa. It seems possible on this evidence that the Pseudopomyzidae and Neriidae are sister groups. Further points of resemblance such as the presence of convergent postvertical bristles and the retention in certain Neriidae of a small but unambiguous vibrissa render this relationship plausible, but, as probable plesiomorphic states for the Neriioidea, they do not provide positive evidence. An alternative hypothesis of a sister group relationship between Neriidae and Micropezidae was supported provisionally by Griffiths (1972), and Hennig (1958) also favoured a close relationship between Neriidae and Micropezidae s.l., without regarding them as sister groups.

## MONOPHYLETIC GROUPS IN PSEUDOPOMYZIDAE

Most authors dealing with classification in the Pseudopomyzidae have been concerned with defining species and genera. Hennig (1969) and Krivosheina (1979) each gave a key to the genera. Krivosheina considered the genera *Pseudopomyzella* and *Heloclusia* to be each isolated within the family by its unusual morphology, and proposed grouping the rest of the genera into the two subfamilies Pseudopomyzinae (for *Pseudopomyza* and *Rhinopomyzella*) and Latheticomyiinae (for *Latheticomyia*, *Polypathomyia*, and, possibly, *Tenuia*). The relationships of *Eopseudopomyza* were not mentioned, and the system was not claimed to be phylogenetic.

In attempting to define groups of pseudopomyzid genera which may be monophyletic, a number of character sequences have been considered, but polarities are often difficult to determine because of the remoteness or independent specialisation of outgroups. The following characters do not appear to be sufficiently stable for group characterisation: development of spaced costal spines, development of vein closing cell bm (second basal), development of prescutellar acrostichal bristles, and, to some extent, development of discal setulae on the scutellum. The position of the preabdominal spiracles is not recorded in all genera, though usually it is within the lateral margin of each tergite. In *Latheticomyia* the lateral margins of some abdominal tergites appear to have undergone desclerotization, a process which leaves the spiracles in an extended pleural membrane. I have not seen specimens of the genera *Eopseudopomyza* and *Tenuia*, and their morphology is known to me only from published descriptions. I do not consider that character sequences in the family are sufficiently understood for production of a cladogram.

The following three informal groups are suggested as being possibly monophyletic, but their status needs further study.

**Group 1**

Fronto-orbital bristles three; setulae near middle of postfrons little developed; cheek with a linear series of setulae; dorsocentral bristles five; anterior intra-alar bristle absent; subcosta distinct to well beyond mid-length of cell c (second costal); cell cup (anal cell) moderately small; distal section of  $CuA_2+A_1$  (vein 6) strong, rather abruptly discontinued well before margin. Included genera: *Latheticomyia* Wheeler (Americas), *Tenuia* Malloch (Philippines).

The group is perhaps characterised mainly by plesiomorphies. The condition of vein  $CuA_2+A_1$  is probably apomorphic in relation to that in group 2, but is not absolutely distinct from that in group 3. The absence of the anterior intra-alar bristle and the less reduced cell cup may be plesiomorphic states relative to those of the other two groups. Hence the group, if monophyletic, may be a sister group to the other two groups combined.

**Group 2**

Fronto-orbital bristles two or three; setulae near middle of postfrons little developed; setulae of cheek not forming a linear series; dorsocentral bristles four; anterior intra-alar bristle usually present; subcosta variable in length; cell cup very small (often incomplete); distal section of vein  $CuA_2+A_1$  gradually fading distally (except in *Polypathomyia*). Included genera: *Heloclusia* Malloch (Neotropical Region), *Polypathomyia* Krivosheina (eastern Palaearctic Region), *Pseudopomyza* Strobl (Palaearctic, Neotropical, and Australasian Regions).

The group includes all those pseudopomyzids with four pairs of long dorsocentral bristles, not intergrading with setulae anteriorly. This is perhaps an apomorphic condition,



as the groundplan condition of the outgroup Cypselosomatidae probably includes the presence of five or more dorsocentrals. (The alternative outgroup Neriidae is regarded as too specialised in thoracic morphology, including chaetotaxy, for comparison).

The delimitation and subgeneric classification of *Pseudopomyza* have been treated by D. McAlpine (1994).

### Group 3

Fronto-orbital bristles four; setulae near middle of postfrons well developed and medially inclined; setulae of cheek not forming a long linear series; dorsocentral bristles five, or becoming indefinite anteriorly; anterior intra-alar bristle developed; subcosta distinct only on about basal half of cell c (second costal); cell cup very small; distal section of CuA<sub>2</sub>+A<sub>1</sub> (vein 6) abruptly discontinued (*Pseudopomyzella*) or apparently more distally prolonged (*Eopseudopomyza*). Included genera: *Pseudopomyzella* Hennig (Neotropical Region), *Eopseudopomyza* Hennig (Palearctic, Tertiary).

This group includes all known pseudopomyzids with four fronto-orbital bristles, with coarse medially inclined setulae near the middle of the postfrons just in front of the ocelli, and all those with three well developed series of anterior intradorsocentral setulae (including acrostichals). These three conditions could be autapomorphies as they contrast with those in all possible outgroups to the Pseudopomyzidae, or at least with their groundplans. The reduced cell cup and presence of an anterior intra-alar bristle suggest a relationship to group 2.

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